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# Baseline and Stress-Induced Levels of Corticosterone during Different Life Cycle Substages in a Shorebird on the High Arctic Breeding Grounds

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## ABSTRACT

After a migratory flight of several thousand kilometers to their high arctic breeding grounds, red knots (*Calidris canutus islandica*, Scolopacidae) showed high baseline concentrations of plasma corticosterone (58 ng/mL). Such high baseline corticosterone levels may be conditional for the right behavioral and metabolic adjustments to environmental and social stresses that shorebirds experience on arrival in an unpredictable tundra breeding environment. Despite the high baseline levels of corticosterone, red knots still showed a marked stress response during the postarrival period, with corticosterone concentrations increasing significantly during a 60-min period of confinement. Baseline levels of corticosterone declined as the breeding season progressed. Red knots with brood patches, that is, birds that had completed egg laying and commenced incubation, had a reduced adrenocortical response to the stress of confinement compared with red knots with no, or with half-developed, brood patches. This is consistent with the idea that birds breeding in extreme environments with short breeding seasons may exhibit a decreased adrenocortical response to

stressful events to prevent high corticosterone concentrations from inducing interruptions of reproductive behavior.

## Introduction

Birds often react to unpredictability in the environment and to energetically demanding events by increasing circulating corticosterone. Elevated levels of corticosterone enable behavior and physiology to adjust appropriately to environmental perturbations that might otherwise compromise individual fitness (Wingfield and Ramenofsky 1999). However, elevated corticosterone concentrations may also reduce fitness. For example, high corticosterone levels suppress territorial and parental behavior and compromise reproductive success (Silverin 1986, 1990, 1998; Wingfield and Silverin 1986). Individuals should therefore adequately tune their adrenocortical response to acute stress on the basis of their physiological state and the precise nature of environmental circumstances. Although hormones other than corticosterone also change in response to stress, an increase in glucocorticosteroid secretion is common to most stressful events and therefore the subject of our study.

Many birds seasonally modulate the sensitivity of the hypothalamo-pituitary-adrenal (HPA) axis to stress (Wingfield 1994; Wingfield et al. 1995; Romero 2001). A reduced sensitivity of the HPA-axis to environmental perturbations has been found in several bird species breeding in extreme environments (Wingfield et al. 1992, 1995; Wingfield 1994; O'Reilly 1995; Silverin et al. 1997; but see Astheimer et al. 1994, 1995). It has been suggested that such a reduced response to environmental stress may be functional in preventing birds from suspending reproductive activities during perturbations that are likely to occur within the short breeding season.

Dictated by the brevity of the arctic summer, shorebirds breeding in the high arctic start reproductive activities shortly after arrival on the breeding sites (Meltofte 1985; Davidson and Morrison 1992). Because past research efforts also suggest a correlation between increased baseline concentrations of corticosterone and long-distance migratory flight in shorebirds (O'Reilly and Wingfield 1995; Piersma et al. 2000), rapid changes in corticosterone profiles soon after completion of the migratory flight are to be expected in arctic-breeding shorebirds. Elevated baseline concentrations of corticosterone pos-

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sibly play a role in adjusting physiology, behavior, and/or general awareness to the potentially arduous and unpredictable environmental conditions both during the flight to and during arrival at the high arctic breeding grounds (Piersma et al. 2000; Landys-Ciannelli et al. 2002).

Despite increasing evidence that the HPA-axis of some birds breeding in severe environments has decreased sensitivity relative to birds that breed in less severe environments, little is known about the exact timing of modulations in adrenocortical sensitivity to stressful events within the breeding season and/or the proximate cues leading to this modulation. We investigated the existence and timing of modulation of baseline concentrations of corticosterone and the adrenocortical stress response in relation to life cycle substage (terminology after Jacobs and Wingfield 2000) of the breeding cycle in a population of red knots (*Calidris canutus*) that breeds in some of the northernmost land on earth, on northern Ellesmere Island, Canada. These red knots reach the high arctic tundra after a direct flight of some 3,000 km from Iceland (Morrison and Davidson 1990; Gudmundsson 1993).

## Material and Methods

### Research Area and Knot Population

Adult red knots were caught between June 1 and August 11, 1999, in the vicinity of a small sewage outlet near the Canadian Forces Station at Alert, Ellesmere Island, Canada (82°30'N, 62°20'W). These red knots belong to the subspecies *islandica* that winters on mudflats in northwest Europe and migrates in spring with one intermediate stop in Iceland to the breeding grounds in Greenland and Arctic Canada (Davidson and Wilson 1992). The majority typically arrives on the breeding grounds between the last days of May and the first week of June (Davidson and Morrison 1992), usually with some fat stores remaining. These stores may provide energy through the first days on the tundra when food resources are scarce. During the postarrival period, when the birds minimize thermoregulatory costs, flock together, and shelter from cold winds (Davidson and Morrison 1992), body masses of both sexes decrease to an average of 120 g, which is maintained during incubation. Courtship and mating takes place rapidly after arrival, and clutches are laid in the second half of June. Incubation, for which both sexes are responsible, lasts 22 d (Nettleship 1968; Tulp et al. 1998). Most females abandon the brood soon after hatching to prepare for autumn migration, leaving the male to tend the precocial chicks.

Birds were captured during three distinct life cycle substages: (1) after arrival on the breeding grounds, (2) during pair bond and territory defense, and (3) during incubation. Only two birds caught after June 8 had not developed brood patches and were probably unsuccessful in finding a partner and/or occupying a territory (Fig. 1D). Therefore, we consider all red knots

caught before June 9 that had not started developing brood patches yet as "recently arrived."

We performed counts of the maximum number of birds observed near the sewage outlet on a daily basis. Additional counts were made in other areas around Alert that we visited when we were searching for nests and broods of red knots. A 1.4-g radiotransmitter that was attached to a female after her capture at the sewage outlet enabled one nest to be discovered and followed in detail.

### Capture Protocol

Birds were caught with several different net types that could be remotely operated. A rocket net and an elastic-powered clap net were used to capture birds on snow-free patches of tundra. We also caught birds with a small manually operated jerk net (Hicklin et al. 1989) and with drop nets (framed nets of 1 m<sup>2</sup> supported on one side by a stick attached to a long, thin rope that was pulled as soon as a bird was underneath).

### Capture Stress Protocol

Blood samples of approximately 70  $\mu$ L were collected into heparinized capillary tubes after the brachial vein was punctured with a sterile needle. All samples were collected within 1–4 min (average: 2 min, 33 s) of capture. These samples are referred to as "baseline." Previous research on captive red knots has shown no significant increase in corticosterone concentrations during the first 4 min after capture (Piersma et al. 2000). We kept birds in cloth bags and collected blood samples at 10, 30, and 60 min after capture to study the corticosterone release into the circulation. This method, known as the "capture stress protocol," measures the responsiveness of the HPA axis to stressful events and presumes that the stress of capture, handling, and restraint represents a uniform and comparable perturbation for all individuals (Wingfield 1994; Wingfield et al. 1995).

An additional 20  $\mu$ L of blood was taken for molecular sexing as described by Baker et al. (1999). The birds received a numbered metal ring (U.S. Fish and Wildlife Service) and a unique combination of color rings, so that individuals were identifiable in the field.

We measured body mass to the nearest gram within an hour of capture using a spring balance. Lengths of the tarsus, the bill (exposed culmen), and the wing (maximum chord) were measured to the nearest millimeter. We determined the extent of breeding plumage (on a scale from 1 to 7, where 1 indicated a full gray winter plumage, 4 indicated intermediate plumage, and 7 indicated complete rusty red summer plumage) and the occurrence of contour feather molt, and we checked for the presence of eggs by palpation. We used the presence and development of brood patches (paired bare regions on the belly that facilitate heat transfer between the incubating bird and the

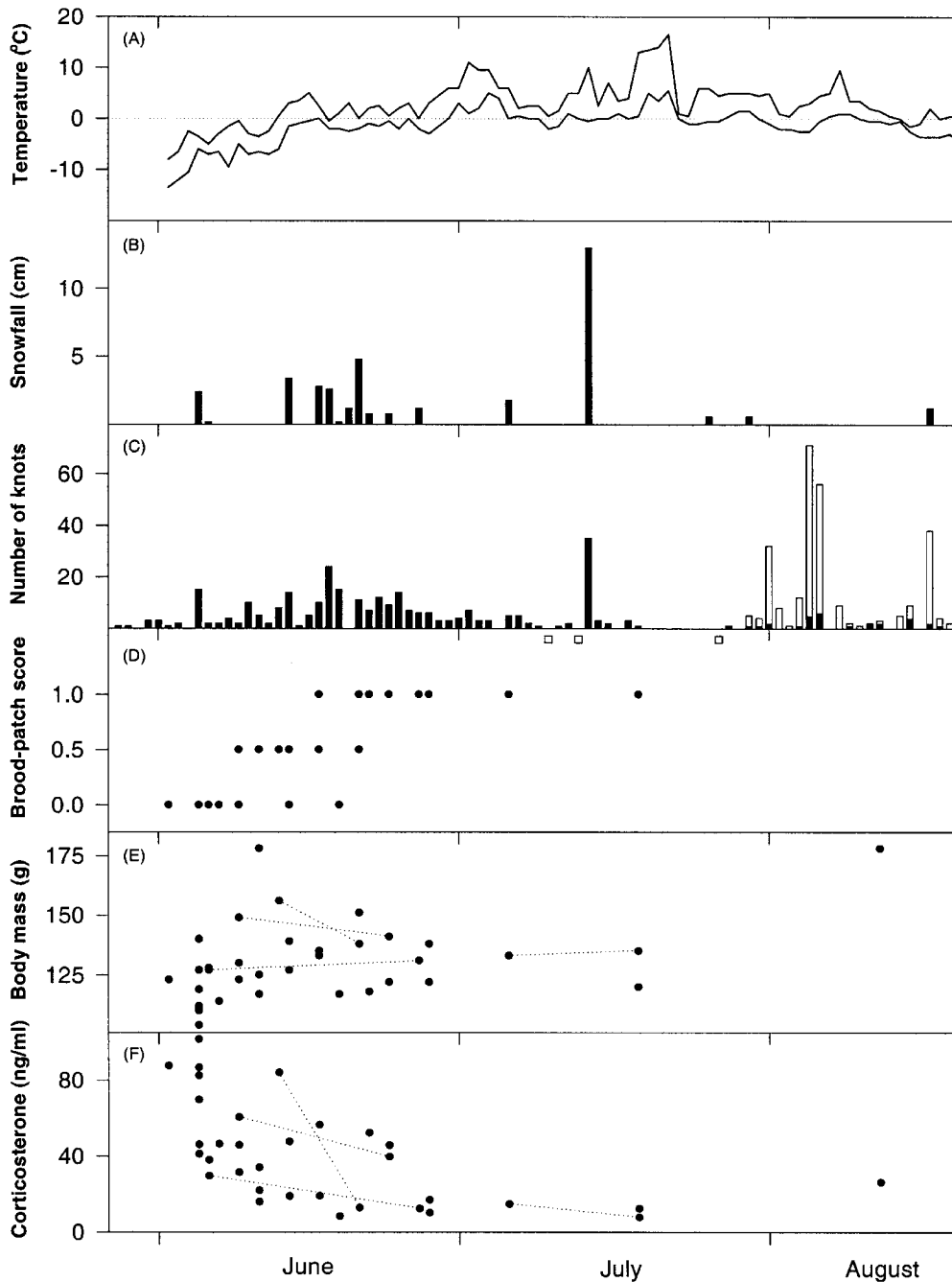


Figure 1. Progress of the summer in Alert, 1999. *A*, Minimum and maximum daily ambient temperatures (°C). *B*, Amount of daily fresh-fallen snow (cm). *C*, Daily total number of observed red knots near Alert; black bars represent adult birds; white bars represent juveniles. *D*, Brood patch scores of the caught red knots (*filled circles*) and known hatching dates of red knot broods (*open squares*). *E*, Body mass (g) of the caught red knots. *F*, Baseline corticosterone concentration of the red knots caught in Alert, 1999. Body masses and baseline corticosterone concentrations of recaptured individuals in *E* and *F* are connected with a dotted line.

eggs) to assess life cycle substage. Both sexes of red knots incubate their clutch and develop brood patches during incubation. Brood patches were scored as 0 (no sign of brood patches), as 0.5 (brood patches are developing but not yet completed), and as 1 (fully completed).

Behavioral observations indicated that brood patch scores are valid indicators for different life cycle substages. Birds captured in early June, which were among the first to arrive in 1999, did not have a brood patch (score 0). Several of the birds with brood patch score 0.5 when captured were seen in close pair bond with their mate on the day of, or days following, capture, which indicated that although they were paired, incubation had not yet started. In addition, two females carrying eggs had not yet completed their brood patch development. This suggests that brood patches do not become fully developed until egg laying is complete. The first knot with a fully developed pair of brood patches was caught on June 16; the start of incubation of two clutches (calculated from known days of hatching) was on June 16 and 19 (see "General Behavior and Progress of the Breeding Season"). We therefore considered that a brood patch score of 0 indicated recently arrived birds; a score of 0.5 indicated birds in the stage of pair bonding, territory defense, and display; and a score of 1 indicated incubating birds.

#### *Radioimmunoassay*

Blood samples were kept cold by the low ambient temperatures in the field for only a few hours until plasma was separated by centrifugation at 6,900 g for 10 min, after which the samples were stored at  $-20^{\circ}\text{C}$  and transported frozen to Seattle for analysis. Plasma levels of corticosterone were measured using specific radioimmunoassay after extraction in 4 mL redistilled dichloromethane following procedures described in more detail by Piersma et al. (2000). Samples were run in duplicate. Recoveries after the extraction with dichloromethane ranged between 77.6% and 100%. Samples were randomly assigned to one of three assays. Interassay variation was less than 20%. Intra-assay variation, as calculated from duplicates, was 5%.

#### *Statistical Analysis and Comparisons*

Corticosterone concentrations were normally distributed and presented as means  $\pm$  SE of the mean. We corrected body masses for size differences by determining the mass residuals from a regression of log body mass on log wing length (slope = 3.844;  $P = 0.022$ ). Sex gave no significant effect in an ANCOVA. Mass residuals of red knots caught at arrival in Alert (before June 9) in several previous years were calculated from this same regression.

Differences in corticosterone stress profiles between three life cycle substages (as indicated by brood patch score), time of day, and sexes were analyzed by a repeated-measures ANOVA,

in which we removed variables that had a nonsignificant effect on corticosterone concentration in stepwise fashion. Neither sex, nor the interaction terms with sex, had a significant effect on corticosterone concentration; therefore, we included two individuals of unknown sex in our analyses. To investigate whether there was an effect on corticosterone concentrations, the times of the day on which birds were caught were assigned to four intervals of 3 h each, covering the period over which the birds were caught (1100–2300 hours); time classes lasted from 1100–1400, 1400–1700, 1700–2000, and 2000–2300 hours, respectively.

One individual captured on August 11 was excluded from the comparisons of baseline and stress-induced corticosterone levels at different substages of the breeding cycle because it was considered to have completed breeding activities and was preparing for autumn migration. Retrapped individuals were only used in the analysis of the stress profiles and considered independent measures when they had reached a new physiological state at the time of retrapping (indicated by higher brood patch score). Whether or not repeat measures of retrapped individuals were used in the analysis did not affect the analytical outcomes.

## **Results**

### *General Behavior and Progress of the Breeding Season*

The first red knot arrived at Alert on May 27, 1999 (Fig. 1C). By the second week of June, the tundra was still almost completely snow covered, and maximum daily ambient temperatures remained below  $0^{\circ}\text{C}$  until June 12 (Fig. 1A). Pitfall traps indicated that insects were not very abundant or active until late June (R. I. G. Morrison, unpublished data). Red knots are known to eat vegetation early in the season (Nettleship 1974) and were observed eating seeds at Alert during early June 1999. We think, however, that the red knots also depended partly on the fuel stores that were left after the migratory flight (Davidson and Morrison 1992). The station's small sewage outlet was probably the only running water in the area in early June, and it attracted many arriving birds. Typically, the early-arriving birds were rather inactive, grouping together in small flocks on the hillsides where they were sheltered from the wind (Davidson and Morrison 1992). Many red knots appeared in the area on June 4. After this date, birds started to sing and to show display flights.

Several arriving birds had rather low body masses (below 115 g) compared with birds captured later in June (Fig. 1E), although red knots are presumed to arrive with some energy stores remaining after the migratory flight (Davidson and Evans 1988; Morrison and Davidson 1990). Residual body masses of individuals caught before June 9 in six separate years (between 1976 and 1999) differed significantly between years (ANOVA,  $F_{5,89} = 3.097$ ,  $P = 0.013$ ). A Tukey post hoc analysis revealed that residual body masses in 1999 were significantly lower compared with only two of the 6 yr, that is, 1987 ( $P = 0.034$ ) and

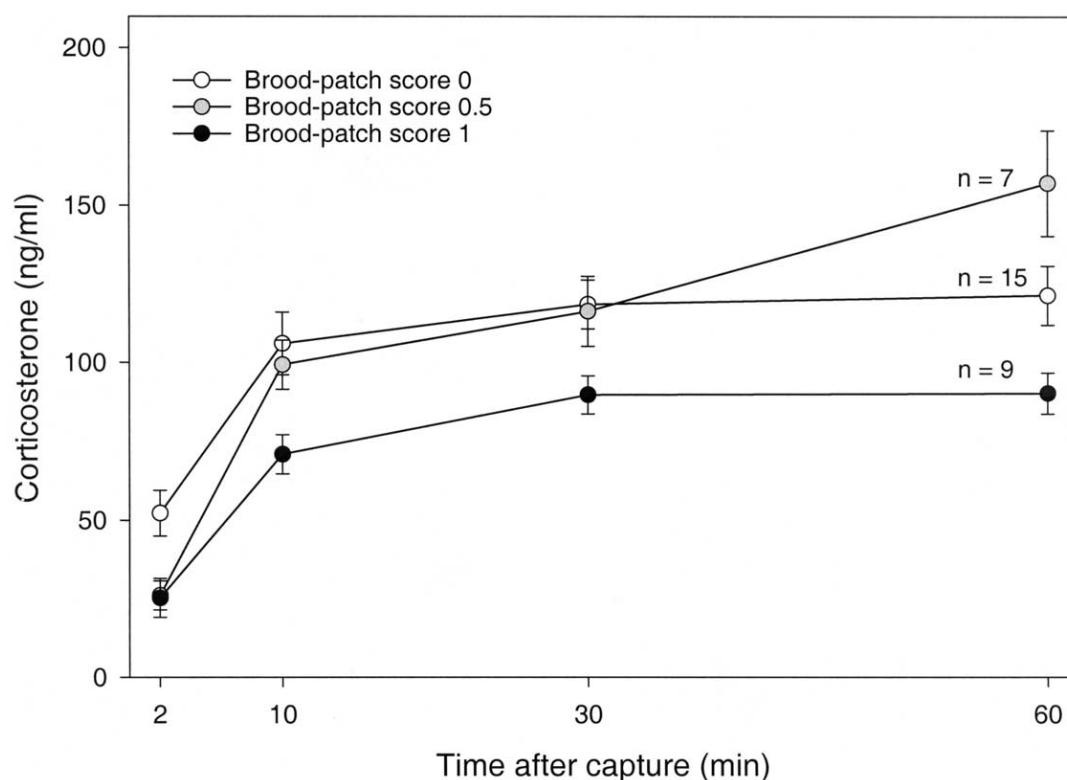


Figure 2. Corticosterone stress profiles in relation to time after capture for individual red knots with different brood patch scores

1990 ( $P = 0.011$ ). The energetic state in which the birds arrived in Alert in 1999 was thus similar to at least three other years.

Soon after arrival, the birds started developing brood patches (Fig. 1D). Two females obviously carrying well-developed eggs were caught on June 10 and 12, with body masses of 178 and 156 g, respectively (Fig. 1E). Red knots probably started clutches on the few snow-free parts of the tundra during this period. The first bird with a completely developed brood patch was a male caught on June 16 (Fig. 1D). This indicates that some clutches were probably complete by then and that incubation had started. During incubation, there was much less variation in body mass between individuals. Birds caught after June 20 had body masses ranging between 116 and 141 grams.

Three clutches hatched on July 8, 11, and 26, respectively (Fig. 1D). Because red knots incubate for 22 d (Nettleship 1968), incubation of these clutches presumably started June 16 and 19 and July 4, respectively. The latter represented a very late clutch with only three eggs. One chick from this nest was followed while flightless and relocated after fledging, eventually appearing at the sewage stream. The bird was very thin and had been unable to build up stores for southward migration in August. When we recaptured it at age 30 d on August 25, some of its breast feathers carried ice crystals, and the bird

weighed only 87 g. On September 1, this individual was killed by a gyrfalcon (*Falco rusticolus*).

#### Baseline Corticosterone

In early June, the red knots showed high baseline concentrations of corticosterone. Baseline levels of arriving birds (caught before June 9) ranged between 22 ng/mL and 101 ng/mL (average 58 ng/mL). During the course of the breeding season, the baseline concentrations decreased; concentrations in the latter half of June did not exceed 60 ng/mL, and after June 25, the maximum measured baseline concentration was 20 ng/mL. All four retrapped individuals showed decreases in baseline levels between captures (Fig. 1F).

Baseline corticosterone levels differed significantly between individuals with different brood patch scores (ANOVA,  $F_{2,28} = 5.207$ ,  $P = 0.012$ ). Tukey post hoc analysis showed that baseline levels of corticosterone for birds with no brood patch (arrival) were significantly higher than those for birds developing brood patches (score 0.5;  $P = 0.048$ ) and for birds with fully developed brood patches (incubation, score 1;  $P = 0.025$ ; Fig. 2). Baseline concentrations did not differ between birds with brood patch scores 0.5 and 1 ( $P = 0.997$ ). Of the

13 recently arrived red knots, six individuals showed baseline levels of corticosterone higher than 60 ng/mL (Fig. 1F). These baseline levels are as high as maximum stress levels of several individuals during incubation (see "Adrenocortical Stress Response"). Baseline levels of corticosterone of recently arrived red knots were not correlated with residual body masses (linear regression,  $F_{1,11} = 0.101$ ,  $P = 0.757$ ).

#### Adrenocortical Stress Response

In all life cycle substages, mean corticosterone concentrations increased as a result of capture and handling (repeated-measures ANOVA, within subjects:  $F_{3,84} = 62.063$ ,  $P < 0.001$ ). This means that despite the high circulating baseline corticosterone concentrations in recently arrived birds, the levels increased further as the result of capture stress, to concentrations of about 120 ng/mL (Fig. 2). Brood patch score had a significant effect on corticosterone concentrations (repeated-measures ANOVA, between subjects:  $F_{2,28} = 8.720$ ,  $P = 0.001$ ).

The magnitude (shape) of the stress-induced increase in corticosterone differed significantly between the different life cycle substages, as indicated by the interaction term "time after capture times brood patch score" ( $F_{6,84} = 2.824$ ,  $P = 0.015$ ). During the incubation period (brood patch score 1), red knots had a less intense adrenocortical stress response than during the preceding life cycle substages on the breeding grounds, with average maximum corticosterone concentrations of only 90 ng/mL (Fig. 2). Inclusion of sex, time of day, and their interaction terms showed no significant effect on the adrenocortical stress response.

#### Discussion

##### *High Baseline Levels of Corticosterone at Arrival on the Breeding Grounds*

Immediately after arriving at their breeding grounds, red knots had significantly higher baseline corticosterone levels compared with levels later in the breeding season. The elevated baseline concentrations of corticosterone suggest a functional relationship with the arrival onto the Arctic tundra. Baseline corticosterone concentrations of red knots arriving in the Alert area are comparable with maximum stress levels that have been found during other (sub)stages of the life cycle in red knots (Piersma et al. 2000; M. Landys-Ciannelli, unpublished results). Nevertheless, corticosterone concentrations of recently arrived red knots were still able to increase in response to capture and handling. This indicates that these well-adapted, long-distance migrants were not unduly stressed by the flight of several thousand kilometers.

Corticosterone plays a role in protein catabolism during fasting and endurance. For example, in a study of 10 passerine species caught in the spring on an Italian island just after a migratory flight of at least 500 km from North Africa, only

individuals with depleted fat stores and critically emaciated breast muscles (an important source of protein) showed high corticosterone levels ( $<45$  ng/mL; Jenni et al. 2000)—levels that were suggested to be associated with increased protein breakdown, as in voluntarily fasting king penguins (*Aptenodytes patagonica*; Cherel et al. 1988). Red knots are usually thought to arrive on the breeding grounds with some fuel (fat and protein) stores remaining (Davidson and Evans 1988; Davidson and Morrison 1992). Our results show that residual body masses of arriving birds were lower in 1999 than in 1987 and 1990, both of which were years in which red knots appeared to arrive with nutritional stores (Morrison and Davidson 1990; Davidson and Morrison 1992). Individuals that weighed less than approximately 115 g on arrival may have reached critical levels of starvation because red knots that were found starved after a long frost flight during severe winter weather in The Netherlands weighed on average  $116.3 \pm 6.5$  g (Piersma et al. 1990). However, as there was no relationship between residual body mass and baseline levels of corticosterone in the arriving red knots, we do not think that we measured any effects of starvation in arriving birds.

Following a long-distance flight, migrating bar-tailed godwits (*Limosa lapponica*) also show elevated baseline corticosterone concentrations on arrival at a stopover site in The Netherlands (Ramenofsky et al. 1995; Landys-Ciannelli et al. 2002). Nevertheless, concentrations were considerably lower in these bar-tailed godwits than in the red knots studied at Alert ( $18.0 \pm 1.6$  ng/mL compared with  $58.2 \pm 7.0$  ng/mL). It is interesting that in the bar-tailed godwits the correlation between (residual) body mass at arrival and baseline level of corticosterone was also absent (Landys-Ciannelli et al. 2002). It would appear, therefore, that the high baseline concentrations of corticosterone of shorebirds after a long-distance flight cannot be attributed to the amount of remaining fat and protein stores alone and may be more related to the unpredictable environment into which red knots arrive (see Piersma et al. 2000).

##### *Suppressed Adrenocortical Stress Response during Incubation*

At the start of incubation, the magnitude of the adrenocortical response to stress became significantly reduced. This is consistent with observations on a reduction in the stress response in passerines caught on their breeding territory in extreme environments with short breeding seasons. It differs from non-territorial passerines or passerines at lower latitudes with longer breeding seasons, which show relatively high sensitivity to environmental stressors, even during incubation (e.g., Wingfield et al. 1992, 1995; Wingfield 1994; Silverin et al. 1997). Although an adrenocortical stress response induces temperate-breeding passerines to respond to stressful events in an adaptive manner, for example, by deserting the nest in response to bad weather or a predator (Silverin 1986, 1990, 1998; Wingfield and Silverin 1986), the short arctic summer does not allow any time for

repeat nesting attempts (Tulp et al. 1998); such responses would result in failed reproduction. Thus, as illustrated by Figure 3, the suppressed adrenocortical response to stress of red knots and some passerines during incubation in the high arctic ensures that relatively small disturbances do not cause nest failure.

#### *Sex-Dependent Modulation of the Adrenocortical Stress Response*

Both sexes of red knots share incubation duties (Tulp et al. 1998; J. Reneerkens, R. I. G. Morrison, and T. Piersma, personal observations), so they both may benefit from a reduced adrenocortical response to potentially stressful events. O'Reilly (1995) showed that among five arctic-breeding shorebird species, the sex responsible for incubation adaptively suppressed the adrenocortical response to stressful events, while the non-incubating sex did not. Species with equal role division were suggested to show no difference in their adrenocortical stress response during incubation. This was confirmed for one species (semipalmated sandpiper, *Calidris pusilla*) but not for another (western sandpiper, *Calidris mauri*) in which males, which spend a smaller proportion of time incubating the eggs, had a significantly higher adrenocortical response. Our data are con-

sistent with the prediction of equally suppressed adrenocortical stress responses in a species with equal role division.

#### *Predictability of the Environment and Corticosterone*

Varying levels of corticosterone may regulate different behaviors (Wingfield and Ramenofsky 1999). Elevated baseline levels are suggested to trigger a sensory preparedness to unpredictable environmental conditions during migration (Piersma et al. 2000; Landys-Ciannelli et al. 2002). Red knots with maximal fuel stores in preparation for northward migration had the highest corticosterone levels (Piersma et al. 2000). Because these birds were far from energetically depleted, it was suggested that baseline levels of corticosterone were elevated in anticipation of unpredictable conditions during flight and at arrival on the breeding grounds. These elevated corticosterone levels should not necessarily be interpreted as "stress" but may reflect an anticipatory mechanism to deal with environmental challenges after arrival on the high arctic breeding grounds.

Successful reproduction in the high arctic depends on (1) a good timing of the migratory flight, (2) sufficient energy and nutritional stores to sustain a migration flight and enable survival after arrival on the breeding grounds when feeding con-



Figure 3. Despite ongoing snowfall, a red knot (subspecies *canutus*) stays on its nest incubating the four eggs. Photo taken on June 27, 1991, at Cape Sterlegova, Taimyr Peninsula, Russia, by Jan van de Kam.



ditions are usually poor, (3) acquiring a high-quality mate, and (4) occupancy of a good territory (Piersma 1987). Elevated baseline levels of corticosterone may help birds respond appropriately to an unpredictable environment. Indeed, it has been shown that red knots subjected to experimentally increased food unpredictability exhibited elevated baseline levels of corticosterone (Reneerkens et al. 2002). Because many negative environmental conditions such as strong winds and poor weather conditions can have deleterious effects on reproductive success (Green et al. 1977; Alerstam et al. 1986; Piersma 1987; Piersma and Morrison 1994; Wingfield et al. 1995), an increased responsiveness to environmental conditions mediated by increased corticosterone levels may help birds to deal appropriately with sudden temporally unpredictable events in the high arctic.

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